THE COURSE OF BIOLOGIC EVOLUTION*.

By Lester F. Ward.

That organic forms are the product of evolution is now not only generally accepted by educated people, but is also fairly well understood as a general proposition. But the special nature of the evolutionary process, particularly the *modus operandi* of the laws of development, is only vaguely or crudely comprehended by any but specialists in some branch of biology, and is not clearly understood by all of these. In proof this I recall a lecture by Henry Ward Beecher, delivered in this city within a year of his death, in which he attempted to expound the modern scientific doctrine of evolution, but in which he showed that he had no adequate idea of what is meant by the arborescent, much less by the dichotomous character of the process of organic development, and seemed to suppose that the progress from monad to man had been one continuous ascending series. He mentioned, for example, as among the ancestors of man, a number of animals belonging to the Ungulata, Carnivora, etc., which are known to be entirely off the anthropogenetic line.

Such crude exposition of so important a law as that of evolution can only react against the progress of its acceptance as a scientific truth, and there seems to be great need that the ex-

*Annual Presidential Address delivered at the Tenth Anniversary Meeting of the Biological Society, January 25, 1890, in the law lecture-room of the Columbian University.

act nature of this law be worked out, and that all attempts to popularize it be correct and be accompanied by the necessary qualifications and an explanation of important subordinate laws. Only thus can the coarse and repugnant conceptions which seem to be taking possession of the popular mind be removed.

EXTINCTION OF TRUNK LINES OF DESCENT.

It is especially important that the first great qualifying principle, which I propose to call *the law of the extinction of trunk lines of descent*, be made clear, since it lops off at one stroke, the most serious of all popular misconceptions. I shall assume that the principle of genealogic dichotomy is clear to the minds of all, since it is nothing more than the simple law of tocogonic descent as exemplified in every human genealogy and every family register applied to all life, except that it relates to species instead of individuals.

Sympodial Dichotomy.—But while organic phylogeny is, in a certain sense, arborescent and dichotomous it cannot be directly compared to any ordinary tree nor even to a plant that branches in a strictly forking or dichotomous manner, such as an *Anychia*, for example. It resembles more nearly that form of indeterminate growth which is termed *sympodial*, in which, instead of the two forks being equal and divergent, one of them has to be regarded as the main trunk and the other as a branch, but in which the branch possesses the greater vigor and vitality and virtually becomes the main trunk, the true stem dwindling, and either dying out entirely or continuing as a reduced and degenerate form. There are many plants, such as the common grape-vine, the houseleek, the heliotrope, and the for-get-me-not, that exhibit this sympodial dichotomy.

Types of Structure.—In studying the operation of this law in biology a number of important facts are to be noted. It is first necessary to consider what may be called *types of structure.* These, in our illustration of sympodial dichotomy, represent first, the main trunk, and afterward the successive branches which become virtually the main trunk. Except in parasitism and other anomalous cases, the development along the main trunk is in the nature of an ascending series of forms, in the sense that the structure grows more and more perfect. There is a differentiation of organs and functions and an integration of parts into organisms of higher and higher capacity, but all are constructed upon the same general plan and represent a single and uniform type. This process of perfectionment in the organisms of original type constituting the main trunk proceeds as far as the nature of that type of structure will permit. The branch which is to constitute the new and higher type is ultimately developed out of this original trunk, but there is no fixed time for its appearance. The original type may have reached its maximum development and remained stationary for any length of time, or it may have already begun to decline before this takes place. In fact it may never take place, but such organisms perish and leave us no history. The branch must possess a higher type of structure, otherwise it must dwindle and also disappear. To give it fresh vigor and power to continue the stock it must have acquired, through the known laws of variation and selection, some advantageous character not possessed by the original type, to which its superior vigor is due. It then in turn continues to develop and goes on improving in the same manner as the main trunk did before it, until, like that, it reaches the maximum limit to its capacity for progress, *i. e.*, until nothing more can come from that type of structure. Like its ancestor, too, it then remains stationary for an indefinite period and eventually declines, and either persists in a degenerate form or dies out altogether. A second branch endowed with still higher capacities is developed from the first and this repeats the process, and so on indefinitely, higher and higher types being successively developed, carrying up the system by this process of ascending sympodial dichotomy.

Persistence of unspecialized Types.—It often happens that the highest organisms of the more ancient types become extinct while the lower or less perfect ones persist and are found mingled with organisms of the higher types that are the dominant forms of life at subsequent epochs. This fact has led those who did not understand the law of types, as just stated, into doubts relative to the fact of development, since the certainty that organisms belonging to types that still exist, but of much higher rank, formerly inhabited the globe gave rise to the belief that there has been degeneracy instead of progress. To escape this error it is necessary to understand that progress takes place primarily through the development of new and higher types of structure, embodying successively higher and higher capacity for improvement, and that the archaic forms belonging to lower types, and therefore, as it were, upon a lower plane of life, unable to compete with those of higher type, are repressed and only appear among the latter as humble, and, as regards their own ancestors, really degenerate forms.

We thus have a series of epochs in the earth's history during each of which a different type has predominated, each later type being higher in its capacity for improvement than its predecessor. You are all more or less familiar with the successive reigns of articulates in the Cambrian, mollusks in the Silurian, fishes in the Devonian, reptiles in the Mesozoic, and mammals in the Cenozoic; and you have doubtless frequently heard astonishment expressed at the great perfection to which the articulated type attained in the Trilobite, the molluscan type in the Ammonite, the piscine type in the Ganoid, the reptilian type in the Dinosaur, and the mammalian type in the mastodon, the highest expressions of all of which belong to geologic periods, and whose living representatives, with few exceptions, belong to the humbler forms of life.

DEVELOPMENT IN PLANTS.

As a specialist only in the lower of the two great kingdoms it is not my place to enter into details respecting the working of these several laws in the animal kingdom, even if I were competent to do so. My illustrations must therefore be chiefly drawn from plants.

It is well known that the three principal groups of modern cryptogams, the ferns, Lycopodiaceæ, and Equisetaceæ, represent the degenerate descendants of a vegetation which formed extensive forests in Carboniferous time, and Hugh Miller, Dr. Lindley, and some more recent authors have used this fact in the manner above referred to, as demonstrating that the life-series of the globe is as likely to be a descending as an ascending one, and that development as a general principle is not proved. Of course it is now well understood that natural selection does not necessarily produce an ascending series, as for example, in parasitic degeneration. But the principle which I have formulated to-night of type degeneracy has been almost entirely ignored, although it is alone able to explain the most important facts that seem opposed to evolution in general. The modern degenerate cryptogamic vegetation is one of those facts and to it I must devote a few moments of explanation.

The so-called natural system of classification in botany is based primarily upon the reproductive function. As founded by Jussieu it was exclusively so based, but De Candolle undertook to introduce a new principle, viz., that of the structure of the axis or trunk, by which he separated exogenous from endogenous plants, and supposed that this line could be drawn between monocotyledons and dicotyledons, erroneously including the gymnosperms in the latter of these groups. The weight of his authority not only long retarded the discovery of the true position of the gymnosperms as the immediate descendants of the crytogams, but it had the further effect of barring out the important truth which vegetable paleontology has at last made clear that there once existed a large class of exogenous cryptogams.

Origin of Exogeny.—It has long been known that the Stigmarias of the coal measures possessed an exogenous structure, and as early as 1839 Brongniart discovered that the stems of *Sigillaria elegans* consisted of a medullary center surrounded by a thin exogenous zone within a thick cortex. The woody zone was shown to be composed of distinct wedges separated by medullary rays. It is now known that nearly or quite all coal plants having the external characters of Sigillaria have this exogenous zone. It was also early discovered that certain coal plants with the general appearance of Calamites exhibit an exogenous structure, and it was at first supposed that these must be something very different, and they were accordingly called *Calamodendron*. Professor Williamson has shown that all true calamites have an exogenous structure of a very definite character. He has also proved that the distinction drawn between Sigillaria and Lepidodendron based on this character is not tenable, since some true Lepidodendra also show the woody zone and medullary rays.

When Brongniart had made the discovery referred to he changed his mind with regard to the plants of the coal measures, and ever afterward maintained that Sigillaria and Calamodendron must be phanerogams, referring them to the Coniferæ. This complete reversal of his former logical and correct views was due to the preconceived opinion that exogenous growth was necessarily correlated with coniferous and dicotyledonous plants, as taught by De Candolle, and there is still a French school of vegetable paleontologists, who, as disciples of Brongniart, continue to maintain that Sigillaria must be placed in an entirely different class from Lepidodendron, and Calamodendron from Calamites, and who are disposed to deny the cryptogamic character of all forms possessing an exogenous structure.

Now the truth seems to be that in the process of development in plants the exogenous structure has been attained in varying degrees along several ascending lines, and that there is a different kind of exogeny in the calamite, the lepidophyte, the cycad, the conifer, and the dicotyledon, while something resembling exogeny has been shown to occur in certain fossil ferns and in certain living monocotyledons. Exogenous cryptogams probably no longer exist. The reign of the cryptogam has come to an end. It occurred in remote Carboniferous times when these plants constituted the greater part of the earth's vegetation. It was then that certain types of the Lycopodiaceæ and Equisetaceæ became forest trees and were supported by exogenous trunks. These types have long since disappeared according to the law of the extinction of trunk lines of descent, and it is only the earlier and simpler types that have come down to us according to the law of the persistence of unspecialized types. The filicine, equisetian, and lycopodian types continued to develop until they reached the highest state attainable by plants having that structure. They even acquired the exogenous character, but only in a rudimentary form.

It would be wholly misleading to place the exogeny of these plants on a par with that of the modern exogen. In the pine and the oak, as every one knows, the bulk of the trunk consists of what we call *wood*, that is, of concentric layers of thick-walled vascular cells, giving to the trunk great strength and resistance, and although in the great sequoias and in the cork-oak the cortical portion, or bark, may attain a thickness of over a foot, still this is a relatively small portion of the entire trunk, and contributes comparatively little to its support. Now, if we imagine a tree in which the bark constitutes the bulk of the trunk and the wood only a comparatively narrow zone close to the central pith, we shall have some idea of the exogenous cryptogamic forest tree of the Carboniferous age. Something approaching it can be seen on a small scale in the first year's growth of a modern exogen, and in most herbaceous plants of that type, and we have another approach to it in the trunks of living cycads.

But when we speak of such thick bark it must not be supposed that we mean the dry corky and flaky exterior which is popularly called bark. This, in the modern exogen, constitutes the greater part of the bark of old trees, but is really the cast-off and, to a greater or less extent, dead matter pushed outward by the annual growth of the bast and liber, or the true live bark of the tree. For every exogen is also an endogen outside of the cambium layer. The bark grows by the deposition of new matter to its interior. It was even so with the exogenous cryptogam, only the endogenous or cortical portion, *i. e.*, the bark, then constituted the greater part of the trunk, whereas it now forms only a thin zone at the periphery.

This difference of degree is so great that it practically amounts to a difference of type, and far back in early Carboniferous time the new type had begun to appear, seemingly along two independent lines, the one typified by the form called Noeggerathia and leading to the modern Cycadaceæ, the other by the form called Cordaites leading to the modern Coniferæ, which two great families rivaled each other for the mastery of the vegetable world during Mesozoic times.

Origin of Phænogamy—Gymnospermy.—It is, however, doubtful whether this great advance in the direction of strength and stability of trunk would have alone sufficed to give these new types the victory in the struggle with the tree-ferns, calamites, and lepidophytes of that epoch. Correlated with it was a still greater advance in the structure of their reproductive organs. The highest types of modern cryptogams only occupy the stage called *heterospory*, i. e., the possession of two kinds of spores, the microspore, or male, and the macrospore, or female spore. That stage was reached by all the higher types of Carboniferous cryptogams. But by a series of steps, which recent researches have enabled us to trace in living forms, the passage was made in that early day from heterosporous cryptogamy to true gymnospermy, and the barrier was crossed which separates the cryptogam from the phanerogam. The origin of true flowers, albeit they were minute, inconspicuous, and devoid of color, fragrance, or beauty, took place at that ancient date. They were some such flowers as our sago-palms and our pines and cedars have to-day. Many fruits have been preserved for us in the coal measures and some of them closely resemble those of the ginkgo or maiden-hair tree. There are other strong proofs that the earliest Coniferæ belonged to the yew tribe of the ginkgo type, a type which is now nearly extinct, having but this single living representative. It was this type, and not the true pines and firs, that represented the conifers during the Jurassic period when the cycadean vegetation predominated over all other forms. And yet this solitary survivor of that long line of ancestors, this waning, tottering, dying ginkgo, with its perfect nut and ample deciduous foliage, may be properly regarded as the highest type of conifers, while the pines, spruces, and junipers must be looked upon as somewhat lower types, persisting according to the law already explained.

Angiospermy.—The next great step was from gymnospermy to angiospermy, the beginnings of which are buried in obscurity. In the gymnosperm the tender developing ovule and maturing seed is exposed to every rude element that besets the life of a plant. Thus exposed it is impossible for it to attain that delicacy of organization necessary to the highest perfection of vegetable growth. Protection of the germ thus early became the great desideratum. When it was first attained we know not, but there are some uncertain indications that angiospermous plants existed in Carboniferous time. But if so they did not belong to the higher or exogenous types. The struggles for the protection of the trunk on the one hand, and for the protection of the germ on the other, were independent struggles. Progress toward exogeny had nothing to do with progress toward angiospermy, and if the latter was attained during Carboniferous or early Mesozoic time it was attained only by endogenous plants, and the earliest angiosperms were endogens and not exogens. That is, the lower type from the standpoint of internal structure became the higher type from the standpoint of floral structure. Progress could therefore only be slow. What was gained by the one was lost by the other. Not until both these steps should be taken by the same type of plants could any new departure take place, and the history of plants shows that it was not until this combination occurred that the great revolution in the vegetable world was brought about.

Exogenous Angiospermy.—The time came at last, we know not at what precise period, when exogenous plants acquired a closed ovary. This is the highest type of vegetation yet reached, and the proofs of its potency confront us every time we behold a modern forest of dicotyledonous trees. The great variety, beauty, strength, and grandeur of this now dominant vegetation amply attest the efficacy of exogeny combined with angiospermy in the attainment of vegetal perfection. Yet the time that elapsed from the beginning of either of these advances, taken alone, to that at which their fortunate combination took place was enormous. Not in the great coal period nor its closing Permian stage; not in the Trias which succeeded did there come forth a single exogenous plant whose germ was thus protected. The great and abundant fossil floras of the Rhetic and Lias of India, Australia, Bavaria, Sweden, and their near equivalents in Virginia and North Carolina, the Connecticut valley, and in both Old and New Mexico, have none of them yielded a trace of any such plant. The same is true of the equally abundant Oolitic floras of Yorkshire, France, Italy, Siberia, and Japan. Not even the highest Jurassic strata of any part of the world have with certainty produced an exogenous angiosperm. The oldest formation at which such plants occur is that on which our own city, the nation's capital, stands, viz., the Potomac formation, whose geological position is doubtful as yet, but if Jurassic, centainly represents the extreme uppermost part of that system. By the author of its flora, Professor Fontaine, it is regarded as the equivalent of the Wealden, which is now commonly supposed to be the fresh water equivalent of the Neocomian or lowest member of the Cretaceous. So late did this now overshadowing type of plant life appear upon the globe. The rapidity with which it advanced, conquering and supplanting all rivals, may be better understood when we remember that it forms eighty-five per cent. of the flora of the Dakota group, which corresponds to the Middle Cretaceous.

A new and vigorous type of vegetation had been developed, the genealogical vine had put forth a fresh branch, the plant world had acquired a new lease of life, and it seems to us, looking back over its history, to have actually taken a leap forward at about this epoch, and ever after to have marched on with enormous strides.

Development of Floral Envelopes.—The resources of improvement in organization were, however, not yet exhausted. The germ was, indeed, now protected, and might acquire within its safe chamber all the subtle shades of perfection possible, but the delicate floral organs by which the fecundation of this germ was accomplished were still exposed, as indeed, it would seem, to a greater or less extent, they must always be. Yet means of their better protection were possible and were gradually adopted.

Apetaly.—The very earliest flowers were probably destitute of any protecting envelopes (achlamydeous), and some such still exist, but most of the lowest types of dicotyledonous plants are provided with one floral envelope, sometimes reduced to a few mere scales, sometimes with several distinct sepals in a whorl around the essential organs, sometimes with these united at the base, and occasionally with a bell-shaped, funnel-shaped, or even tubular calyx. Such plants are called apetalous or monochlamydeous. Paleontology shows that those forms which are now apetalous, especially those in which the flowers are borne in catkins, or are nearly altogether naked, prevailed in early times over those provided with two sets of floral envelopes, which is far from being the case at present. Our law, too, is here again exemplified in the great perfection attained in those early times by such apetalous trees as the poplar, the plane-tree, the fig-tree, the laurel and the sassafras.

Polypetaly.—The next step was the development of a second floral envelope, which, however, had its beginnings in small, strap-shaped, or even bristle-shaped petals. In our current botanies as prepared by Gray, De Candolle, and Bentham and Hooker, the plants having separate petals, or polypetalous plants, such as the rose, buttercup, mallow, etc., are placed before those having the corolla all in one piece, like the morning-glory, honeysuckle, etc. This position is given them to indicate that the authors of these books regarded them as of higher rank. But the geological history of plants teaches that such, at least, was not the order of nature in their development. It shows that polypetalous plants were very early developed. We find them at the earliest epoch at which dicotyledons begin to appear in any great abundance. It is true that we rarely find the flowers, and cannot say with certainty that they were the same as they are to-day. It is quite possible that trees of Cretaceous time whose leaves resemble those of modern polypetalous genera may have then had wholly apetalous flowers, but this is as yet mere speculation.

In this group we have another fine illustration of the law which I have stated, according to which the highest attainable development of any given type of structure is early and rapidly acquired. We are in the habit of regarding our magnolias, our tulip-trees, and the Australian eucalypts, as among the finest specimens of polypetalous plants, and yet the genera Magnolia, Liriodendron, and Eucalyptus appear and are rather prominent in the Middle Cretaceous floras of Europe, Greenland, and America. There was some doubt until recently whether the Eucalyptus really was an American type, so remote is its present home. But during the past summer a member of this Society, Mr. David White, has conclusively demonstrated that these trees flourished in abundance on what is now Martha's Vineyard during the Cretaceous age. They probably extended over the entire western world in that vast antiquity before the human race had made its appearance on our planet.

Gamopetaly.—There was one other step to be taken, the step from the polypetalous to the gamopetalous flower, from a corolla consisting of numerous distinct petals forming a whorl around the stamens and pistil within the calyx, to a corolla consisting of a single piece in the form of a bell, a funnel, or a tube, more and more completely protecting the essential organs. The older botanies call such plants *monopetalous*, emphasizing the fact that the corolla is of one piece, but wholly ignoring the process by which it became so. In fact, by placing this group after the polypetalous one they suggest that they are lower in rank and that monopetalous plants may have become polypetalous by division of the corolla into numerous petals. The German investigators, however, have shown by embryological study that the movement has been in the other direction, the petals of polypetalous plants, having, as it were, united into a corolla, and this is confirmed by paleobotany in showing that polypetalous plants antedated monopetalous ones in the history of plant development. The later botanies, therefore, so far recognize this truth as to adopt the term *gamopetalous* to express this union or wedding of the petals.

The progress from polypetaly to gamopetaly had only begun when the geological record closed. Only a few gamopetalous fossil plants have been discovered. There is reason to believe that there were persimmons, whortleberries, olives, and arrowwoods, during Tertiary times, but most of these have small flowers, and in some of the living representatives the lobes of the corolla are cleft nearly to the base, suggesting that at an earlier period in their history they may have really been polypetalous. The more typical Gamopetalæ, with tubular or funnel-form corollas are for the most part unrepresented in the fossil state, and we must regard these plants as among the latest products of development in the vegetable kingdom.

Nature of Vegetal Development.—I have now endeavored to trace the progress of development in the vegetable kingdom from its earliest beginnings in cryptogamic life to its highest and latest expression in the gamopetalous dicotyledon, with a view especially to showing by what particular steps it has taken place, and how the two laws of the extinction of trunk lines of descent and the persistence of unspecialized types have combined to bring about the varied and abundant vegetation with which the earth is clothed. I have sought to emphasize the fact that this evolution has not been in a single ascending series, that the plants that have one after another succeeded to the mastery have each in turn attained the highest development possible to their respective types of structure and have then surrendered their sceptre forever to the new and more perfect types evolved from them, and have usually dwindled down to comparative insignificance but persisted on in some of their lowest forms. I have wished to make clear and patent the important but rather recondite and popularly little understood truth that biologic progress takes place through this sympodial dichotomy, and not by true dichotomy, much less by the ordinary monopodial branching represented by the common figure of a tree. In other words the phylogenetic tree is something considerably different from the common genealogical tree. It further and especially differs in being exceedingly irregular in the intervals of branching. Expressing the process in time we observe that vast periods pass in waiting for the working out of the most simple principle, which, when once hit upon, produces a complete and rapid revolution in an entire department of life. I can liken it in this respect only to the progress of mankind as brought about by great mechanical inventions made at irregutar intervals and producing undreamed-of revolutions in the whole industrial frame-work of society. The length of the stationary periods in biologic evolution is determined by no fixed law. When a type of structure has advanced as far as it is capable of developing it remains stationary as long as nothing interferes with its continuance. If no change should take place in its environment it might continue for an indefinite period. As, by hypothesis, it can advance no farther it can only vary in the direction of deterioration or extinction. The type of structure once fixed can never change. Only the degree of vigor, luxuriance, or abundance can undergo modification. Deterioration is everywhere illustrated by the present cryptogamic vegetation. The Carboniferous forests of Lepidodendron and Calamites are represented by our little club-mosses and scouring rushes, although they must have descended from trunk lines which had not yet acquired the exogenous structure. Extinction is exemplified by the absence of exogenous cryptogams in the living flora, as also of most of the later cycadean and coniferous types. There are several interesting cases of partial and rapidly approaching extinction. Among such may be mentioned the maidenhair-tree, the mammoth and redwood trees, and also, it would seem, the tulip and plane trees, all of which in their turn dominated the vegetable kingdom, but now, though undiminished in vigor or structural perfection, have been restricted in range, reduced in number, and nearly crowded out of existence.

We have seen that the deterioration or extinction can be only brought about by a change of environment. The only cause for the predominance of a type is its greater adaptation to the existing environment. If undisturbed any given type of structure will equilibrate in the direction of greater adaptation until this is no longer possible. But complete adaptation, as I long ago pointed out,* is impossible. It is always possible for a new type to appear which shall respond more exactly to the surrounding conditions. The environment, it is true, may undergo unfavorable changes. The climate may change, or the type in its migrations may encounter unfriendly influences. Most effective of all is the ever-changing influence of the contemporary life with which a type must come into competition. It must, as we have seen, eventually encounter as a rival in the race for life, the new type which is to succeed it, endowed with elements of new life and with fresh powers both to overcome hostile influences and to utilize the resources of nature. Such superior types, as already shown, are ever and anon arising, proceeding from quarters least anticipated, appearing without regularity either as to place or time, springing sympodially from the original trunk, rising impiously above their parents, and ultimately overshadowing, repressing, crushing, and extinguishing the former lords of the vegetable kingdom. Such in brief is the generalized history of the rise and fall of empires in the world of plants.

What has thus far been said is perhaps sufficient to render clear to most minds the peculiar and complicated character of biologic evolution in general, and to show how widely it differs

* American Naturalist, February 1881, p. 89.

not only from the current crude popular conception of it, but also from the ideas which prevail among well informed and even scientific persons. I need not, I am sure, apologize in this age of specialists, for having confined myself almost exclusively to that kingdom of life with which I am most familiar. I believe that I can safely assume that the zoologists present, in whatever branch, have been able to parallel all the illustrations which I have given by similar ones in their own departments, leading to the same general conclusion.

EXTRA NORMAL DEVELOPMENT.

Thus far I have only taken account of what may be called the normal or legitimate causes of such advantageous modifications of structure as have resulted in the successive upward steps which organic life has taken in the course of its history. But there is another class which may be called extra-normal, abnormal, or even illegitimate causes. Normal or legitimate causes are such as result in the production of characters which are of direct use to the organism. In extra-normal or illegitimate causes the characters produced are such as have only an indirect effect. Thus in the vegetable kingdom normal development tends chiefly in the direction of strengthening the stem, increasing the foliar surface, and protecting the germ and reproductive organs, *i. e.*, in the direction of strength, nutrition, and reproduction, these being the three prime essentials of existence. The various modes of strengthening the trunk, and especially the attainment of complete exogeny, as seen in the trees of the present day, directly improved the conditions of existence and the chances for further development. The gradual attainment of broad appendicular expansions called leaves increased more and more the power to decompose the carbonic dioxide of the air which is the chief nourishment of plants. The separation of the sexes, the transition from spore-bearing to seed-bearing plants, the development of a closed ovary for the protection of the germ, and of floral envelopes for the protection of the stamens and pistils, all tended to perfect the reproductive function and render a higher type possible. These influences were therefore all normal and legitimate in acting directly upon the essential properties of the organism; and had no extra-normal or illegitimate influences come in to modify the results these direct ends would have been the only ones attained. Vegetation would doubtless have still been green as now, there would have been forests of large trees with strong solid trunks and umbrageous foliage; there would have been green grass and rushes, rank and luxuriant herbage, stately palms and graceful ferns, even as now, but this would have been all. Two of the leading features of the actual vegetation would have been wanting, viz., showy and fragrant flowers and highly colored, pleasantly flavored, and nutritious fruits.

A large, showy, or fragrant blossom is of no direct use to a plant. Indeed its nourishment is an expense to the normal growth of the plant. Still greater is the cost of the abundant nutritious matter in many fruits. In both these cases the value to the plant is indirect, and when we study the subject deeply we find that the cause of the development of such organs is a sort of teleological or final cause. Beautiful flowers and edible fruits are extra-normal or illegitimate products of nature, and those who fail to see this have but a crude and imperfect conception of the course of evolution.

Fortuitous Variation.—In a certain sense every influence that affects an organism is legitimate, and we have seen that the several great types have been brought into existence by the improvement of the special opportunities offered by the environment. We have also seen that these opportunities have presented themselves at long and irregular intervals, and, as it were, by chance. In this sense there is only a difference of degree between these normal and legitimate influences and those which I have called extra normal or illegitimate. Their occurrence was fortuitous. They were the result of accidental variations in an advantageous direction seized upon by nature for the creation of higher types of life.

There is a school of evolutionists who maintain that this is the only way in which progress takes place. This is held to be the strictly Darwinian view, as opposed to the Lamarckian view that the "appetencies," as Lamarck called them, *i. e.*, the individual efforts, strivings, and struggles of the organism in advantageous directions, aid in determining what the new and improved type shall be. In a paper which I had the honor to read before this society over a year ago on "Fortuitous Variation as illustrated by the genus Eupatorium" * I endeavored to show that this fortuitous variation was often successful even when no apparent advantage could result therefrom. The tendency to vary is in all directions, as from the center toward the surface of a sphere, and variation will take place in every direction which does not prove so disadvantageous as to render life impossible. In by far the greater number of cases the advantage or disadvantage is slight or imperceptible, and changes go on without improvement or deterioration, causing a great number of equally vigorous forms to arise, all differing more or less from one another. This accounts chiefly for the varied and manifold in nature, and but for this law, hitherto, so far as I am aware, unobserved, nature would be

* See abstract (all that was published) in Nature (London) for July 25, 1889 (Vol. XL, p. 310).

monotonous and uninteresting. From the esthetic point of view, therefore, this is the most important law of biology.

What is its importance from the scientific point of view? As you probably all know, there has been going on during several years past a very lively discussion of the principle of natural selection, and that principle has been vigorously attacked by a large and highly respectable class of working naturalists. Its vulnerable points have been fearlessly exposed and its defenders have been put to their wits' end to save it from serious impairment. It has seemed to me that their mode of defense was ill-chosen and that its weakness consisted in claiming too much for natural selection, more than it can justly be shown to accomplish. The weakest link in the chain is the first one, as Darwin himself admitted, and it seems strange that he, who maintained that the variations which natural selection seizes upon to the advantage of the organism are fortuitous, should not have conceived that these might go on as they begun for a long time and result in important changes that were neither beneficial nor injurious. Those who question the principle of natural selection insist with apparent justice that the incipient changes due to accidental variation during a single generation are utterly inadequate to perpetuate and multiply themselves, that their utility must be infinitesimal and practically nil; and they pertinently ask how the machinery of natural selection was ever set in motion. Strange as it may seem, the defenders of natural selection have thus far found no better answer to this argument than to deny its force and to maintain that every variation, however slight, if in the direction of utility, begins to operate from its inception and goes on increasing with cumulative strength. This answer is not satisfactory and its inadequacy has been sufficiently proved. It should be abandoned and some other substituted, and until this is done natural selection will continue to lack a solid basis upon which to rest.

But it seems to me that there is an answer to the objection, and one which fully meets it. This answer is nothing more nor less than the patent fact already stated that fortuitous variation actually does go on at all times, in many directions, and to great lengths, without any perceptible change in the degree of adaptation which the varying forms have to their environment. I have shown how this takes place in one important genus of plants, and it would be easy to extend the observation to almost any other genus. I doubt not that the animal kingdom is also full of examples.

Here then we have the solution of by far the worst difficulty in the way of natural selection. The beneficial effect need not be assumed to begin at the initial stage. It need not be felt until well-formed varieties have been developed without regard to any advantage in the particular differences which they present. There seems to be no flaw in this mode of solving this paramount problem, and if it is objected that it amounts to a new explanation of the origin of species, I am ready to admit it, and I believe that more species are produced by fortuitous variation than by natural selection. Natural selection is not primarily the cause of the origin of *species*; its mission is far higher. It is the cause of the origin of *types of structure*, such as those whose history I have endeavored to trace, and through which alone biologic evolution takes place.

Extra-Normal Influences in the Vegetable Kingdom.—Returning from this important digression to the subject of extra-normal influences in the vegetable kingdom, let us inquire more closely into their exact nature. As already remarked, the most important are those which have resulted in the development of beauty and fragrance in flowers and of bright colors and agreeable flavors in fruits. But these are by no means all, and we must thus account for most burs, spines, thorns, and other forbidding features, viscid and glandular hairs, as in the sundew, and irregular and peculiar forms of leaves, especially such as are seen in the pitcher-plants, and a great variety of other structures not connected with the reproductive function.

What then are these supra-normal or illegitimate causes which result in such peculiar products? In the first place they consist in special changes in the environment which are seized upon to the advantage of the plant. Plants in view of their stationary character, had especial need of two things, viz., *cross-fertilization* and *dissemination*. Growing together without power to change their position and mingle with remoter forms, there was perpetual danger that close interbreeding might deteriorate or destroy the stock. The seeds of such stationary organisms perpetually falling in the same spot tended to choke one another and to weaken and restrict the species. Every normal and legitimate means of averting these two dangers had been adopted by the earlier types of vegetation. The spores of cryptogams and the pollen of conifers were made so light that the winds would take them up and waft them to great distances. Certain grasses and other herbs were endowed with the peculiarity of being uprooted by the wind at the proper season and blown for miles over the plains, scattering their seeds. And even water had become and still remains a medium for the transportation of both pollen and seed from place to place and from shore to shore. But still these instrumentalities fell far short of the needs of the vegetable world in these directions. At last, and nearly at the same period in the earth's history, two new, and, one may almost say, unexpected agencies came forward, adapted respectively to the supply of these two prime necessities of the plant—viz., *insects* and *birds*.

Origin of Showy and Fragrant Flowers.—Away back in the dim darkness of the coal period when tree-ferns, calamites, and giant club-mosses, combined with archæ-typal yews to people the steaming swamps of a hot, cloud-laden island world, there existed a strange form of insect which can only be compared to the cockroaches of our day, but which seems to have embodied in its structure the beginnings of all the varied types of insect life, the promise and prophecy not only of our dragonflies and beetles, but also of our flies, bees, and butterflies. And during the long ages that followed, while the plant life was passing through the history which I have briefly sketched, the insect world was experiencing a similar unfolding, and new and improved types, very much as in plants, were coming into existence, attaining their maximum development, and giving way to still higher ones, until some time in the late Jurassic or early Cretaceous age forms began to appear which were adapted to obtain sustenance from the pollen, and perhaps from the stigmas of flowers. To do this they were obliged to pass from flower to flower and would unavoidably carry the dust that adhered to their heads, wings and feet from one flower to others more or less remote. Cross-fertilization, that "secret of Nature" discovered by Sprengel, was thus effected, and new vigor was instilled into those forms which for any reason had been so fortunate as to attract these winged friends. We can figure to ourselves a rivalry springing up among plants as to which should offer them the greatest inducement, and through the action of natural selection, which here found a typical field for its normal operation, the entire nature of flowers underwent a rapid change. To continue the figurative expression, all flowers vied to excel in beauty and attractiveness; for these tiny insects possess esthetic tastes which do not materially differ from those of mankind.

To size, showiness, and beauty of coloration, was often added fragrance which was especially successful with moths and other nocturnal insects. Many special inducements were held out. Sweet and nutritious nectars were secreted from the petals to lure on the unsuspecting creatures, and deep, and peculiar grooves, sacs, and spurs were developed to hold this nectar in large quantities. These nectaries were so adjusted that no bee could enter without passing directly over the stigma and brushing upon it the precious dust of other flowers. Wonderful contrivances thus came into existence to secure this supreme end of plant being, and the present world of flowers was ultimately evolved.

The profound modification accomplished by this agency was not confined to size, color, fragrance, and the secretion of nectar. The forms of flowers underwent in many cases a complete change, and an infinite number of wonderful irregularities appeared, varying from the slightest differences in the petals to the amazing abnormalities of the orchids, all calculated to adapt plants to the useful ministrations of insects, sometimes, as in the yucca, to those of a single species of insect without which reproduction is impossible.

And thus it has come about that the form of every flower has its special meaning which can be interpreted by those who have penetrated this great secret. We hear of the language of flowers—that the rose signifies beauty, the daisy innocence, the violet modesty, the myrtle love—but science has discovered a new and real language which the flower not only speaks but writes in clear characters, and which the botanist deciphers and reads by much the same methods that the assyriologist employs when he deciphers and reads the arrow-head inscriptions upon the tablets of Nineveh.

It is thus that flowers are accounted for by modern science in all their beauty and variety. The old idea that they were made for man to admire and enjoy is exploded, and yet it remains true that they were made to be admired and enjoyed by creatures capable of admiration and esthetic pleasure. It is not true that any flower was ever "born to blush unseen" or "waste its fragrance on the desert air." There is a standard of taste so universal that what pleases the bee, the ant, and the butterfly, also pleases the senses of man. Biology has overthrown the anthropocentric theory as astronomy has the geocentric, and every creature lives in and for itself and shares with man to some degree the sublime attributes of mind and soul.*

Origin of bright-colored and sweet-flavored fruits.—In seeking the origin of fruits we have to consider an almost parallel history of development to that which we have been studying in accounting for flowers. But here we must look to another kind of animal life, chiefly to the great family of birds. There were probably no bright-colored or sweet-flavored fruits until the close of Mesozoic time, because the future birds were as yet reptiles crawling over the ground or swimming in the waters, albeit some of them already possessed the inchoate attributes of their avian successors. Moreover, the vegetation of that early period was incapable of employing the intervention of winged life for its distribution. At first it consisted exclusively of spore-bearing plants whose dissemination was chiefly affected by the wind, and which depended upon the infinite multiplication of spores to make up for defective means of distribution. Later came on the gymnospermous types of cycadean and coniferous life, neither of which are now to any great extent adapted to the uses of the feathered world. Paleon-

* Here and later on I use the term *soul* in the sense of conscious desire strong enough to induce active effort for its satisfaction.

tology, both vegetable and animal, thus doubly confirms the view that fruits, in the sense here employed, had their origin simultaneously with the appearance of birds, as flowers did with that of flower-frequenting insects, toward the close of Mesozoic time. Attracted by their bright colors correlated with pleasant flavors, birds learned to visit the plants that bore such fruits. Flying thence to distant parts and voiding the hard seeds of berries and stones of drupes, they became the effective instruments for the dissemination of these forms.

The great problem of distribution was thus solved by bird life as was that of cross-fertilization by insect life, and just as plants vied with one another to attract insects to their flowers, so did they also vie with one another to attract birds to their fruits. Here again it was the universal esthetic faculty that enabled the ancient bird life to prepare the earth for human habitation, and yet, no more than in the previous case was man the final cause. So uniform is the standard of taste throughout the psychic world that what contributes to the pleasure of a bird or an insect also supplies some esthetic want in the race of men.

ABNORMALITIES OF SEX.

There is one other abnormal or supra-normal influence in the organic world which is so important and so well illustrates the principle now under consideration, that it seems proper briefly to advert to it. I refer to the causes which in many cases, particularly in the animal kingdom, make one sex differ so widely from the other.

An array of facts taken from asexual life and from the very early stages of sexuality converge to show that primarily and normally the female is the main trunk line of development, while the male is merely accessory, and need have no importance apart from the reproductive function. Such restriction actually exists in a great many of the lower organisms and in some that are quite highly organized, while throughout the invertebrate world the physical superiority of the female is the rule and that of the male is almost unknown. Female superiority is also the rule and male superiority the exception among all vertebrates except birds and mammals, and sometimes occurs even in these. Normal or legitimate development would make it universal. But in most birds and mammals, the opposite state of things exists, viz., male superiority, and we are so much more familiar with these two highest types of life that the impression is almost universal that the male sex is in some way the primary and dominant one. I shall not waste your time in attempting to refute this popular impression. Those who defend it simply display their lack of acquaintance with the lower forms of life. My own attention was drawn to the subject by certain remarkable phenomena presented by plants, but a study of the very early stages of animal life is sufficient, with the least reflection, to set the whole question at rest.*

The problem is, therefore, to account for this apparently abrupt reversal of the normal process of development as it went on prior to the advent of birds and mammals. What was the extraneous and illegitimate agency which began to operate early in the development of avian and mammalian life? The one term which most nearly expresses it is *sexual selection*, proposed by Darwin. In my opinion the discovery of the principle of sexual selection has equal if not higher rank

* For a fuller, though popular, treatment of this subject, see the *Forum* for November, 1888, Vol. VI, p. 266.

than that of natural selection, since its influence when fully understood will be found to be as great, and to Darwin alone is due the entire credit of making it known. Strangely enough Dr. Alfred Russel Wallace, who simultaneously and independently worked out the law of natural selection, is disposed, as shown by his recent work on Darwinism, to reject sexual selection altogether as a factor in biology ; yet to my mind, it remains debatable which of these two great laws has exerted the more profound effects in modifying the course of organic development. It certainly cannot be said of natural selection that it has produced a complete revolution in that course, or has, so to speak, reversed the wheels of biologic progress, as sexual selection has done ; not in the sense of producing a retrograde movement, but in that of shifting the axis of evolution, if I may be allowed the expression, from its normal position to a wholly abnormal one, and raising to a prime factor what was originally a mere incident in the history of organic life.

Female Selection.—But by sexual selection Darwin meant only *female selection*, which would be the more accurate expression. It was not until the era of birds and mammals that the female really began to exercise a choice, or if, as is proved in a few cases, the females of lower creatures did exercise a choice, the result was the same as in the higher, the superiority of the males.

You all understand this law too well to make any explanation of its operation necessary, and I only desire to bring it forward as one of the most important of all the abnormal or illegitimate influences that have brought about the present state of things. I also wish to point out its analogy to the other two influences which I have considered. For here again, size, strength, and beauty, as displayed in the males of so many animals and birds, are the products of a dawning and growing esthetic sentiment, the expression of a developing taste, which is so nearly identical with the most highly developed tastes of mankind that there are no higher objects of human admiration than the gorgeous plumage of birds or the graceful forms of animals—than, for example, the feathers of the ostrich or the antlers of the stag.

Male Selection.—The reign of female selection has been a long one, and throughout the two classes of animals in which it is chiefly displayed it still prevails in full force. It is probably still the dominant influence in the human race, even among its highest types, though here resulting more in mental than in physical superiority in men.

But there are signs that this may not always remain so. I long ago pointed out * that among the higher races of men a form of *male selection* has already begun to exert a strong influence. In civilized life the choosing is not left wholly to women, and with the progress of culture and refinement this mutuality of selection grows more and more marked. That male selection will prove equally effective with female selection is already proved by the ever increasing beauty of women under its influence; and those who think men perverse because they prefer beauty to all other qualities, or women trivial because they make their personal appearance a leading aim of life, have never learned the great law of nature which overrules all the trite maxims of the purists, that beauty means worth—perfection—and that beautiful companions insure perfect offspring, an improved posterity, and a better and nobler race, of men as well as women. And this is why the love of and preference for the beautiful has a higher and a deeper sanction in the everlasting order of things than can be given by any church, any court of law, or any code of morals.

* Dynamic Sociology, 1883, Vol. I, p. 613.

THE PSYCHIC ELEMENT.

In all the cases considered of what I have denominated extra-normal or illegitimate influences affecting the course of biologic evolution, there is revealed to the careful student a common principle to which their peculiar character is due; a certain element of power and independence which gives to them both their anomalous and eratic character among organic laws, and also their remarkable efficacy and success in accomplishing the ends of evolution itself. What is this common principle, this element of power? It is expressed in the single word *psychic*—I had almost said, in the one word *mind*. Philosophers correctly identify these conceptions, and anything that transcends the purely vital partakes of the attributes of mind. This new force, manifesting itself in at least three prominent ways at almost the same time in the earth's history, and producing such astonishing revolutions, was the psychic force beginning to respond to a long process of cephalization, or brain-enlargement, in the animal world. It represents the birth of the soul in nature; it was the response to a demand for the satisfaction of wants, of instincts, of tastes; it was the first expression of purpose and of will. For these are the attributes which led the bee to seek the nectar from the flower, the bird to visit the brilliant cluster of fruit, or the female of the higher creatures to choose the most beautiful male for its mate. And these are psychic qualities and represent the subjective half of the world of mind—the great heart of nature.

The strictly biologic record properly closes here. To show that this same force continues to produce its unlooked-for effects at a higher stage of development, operating from the objective side, through the intellect, or head of nature, and that the results have here been as much more surprising and far-reaching as the organisms through which they were accomplished were higher in the scale of development,* though an easy task, would not only carry me too far, but would trench upon the domain of anthropology and belong more properly to a sister society.

Cosmic Epochs.—Taking a retrospective view of the entire field of evolution and bearing in mind its uneven course as I have sought to depict it, there may be discerned, standing out prominently above all the minor fluctuations, a few great cosmic crises or epochs, in which the change appears so abrupt and so enormous as to suggest actual discontinuity. Three such cosmic epochs belong to the history of life on the globe. The first was the origin of life itself. The second was the origin of soul or will in nature. The third was the origin of thought or pure intellect. While I do not say that any of the factors producing these epochs came suddenly into existence, or that any definite lines exist separating life from soul or soul from intellect, theoretically speaking, the general fact remains that they are practically distinct principles, having diverse effects, originating at widely different periods in the earth's history, and succeeding one another in the order named. Of these three great principles, life, soul, and intellect, and of the cosmic epochs which they have produced, I have in the closing part of this address, attempted to consider the second only, and I have chosen it chiefly because its bearing upon evolution appears to have been wholly ignored or misunderstood. Soul or will is simply desire in the act of seeking satisfaction, and I once presented the evidence to show that this is a true natural force,† obeying all of the three Newtonian laws of motion; but its effects, compared with the other forces of cosmic and

* This is the "indirect method of conation." See Dynamic Sociology, Vol. II, p. 99.

† Dynamic Sociology, Vol. II, p. 95.

organic evolution, appear to us erratic or even spasmodic. Nevertheless its potency is far greater and the ends attained through it are upon the whole the same. It owes this character to the fact that it is a psychic force as distinguished from either physical or vital forces. Its study is therefore a part of psychology, and from it we should learn that psychology is simply a branch of biology and its study should begin with animals and not with man. Finally, the peculiar character of this psychic influence is due to its being a product of higher organization. Mind is to biology what protoplasm is to chemistry. Psychology is transcendental biology.*

* So called by Auguste Comte, who refused to recognize it as a distinct science. See his Philosophie Positive, Vol. IV, p. 342.